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Further studies of the orange rusts of Rubus in the United States

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(WITH FIVE TEXT FIGURES)

INTRODUCTION

The writer's previous studies of the orange rust, showing that the *Caeoma* spores in material from New York, Illinois, Missouri and Wisconsin (6, 7) germinate like teleutospores, left the question as to the relationships of *Puccinia Peckiana* Howe unsolved.

Fischer (5) has recently tested the germination of the aecidiospores of the European *Gymnoconia interstitialis* (Schlecht.) Lagerh. He obtained long germ tubes having all the characteristics of ordinary aecidiospore germ tubes. No promycelia were observed and no cross walls were to be seen in any of the tubes. In one case a thinner tube that resembled somewhat a long sterigma developed at the end of a germ tube. This he thinks may have been the result of growth disturbances. Fischer also made infection experiments and obtained *Puccinia Peckiana* by sowing the aecidiospores on supposedly healthy plants of *Rubus saxatilis*. His results, taken in connection with those of Tranzschel (13), Clinton (3), and Liro (9), give strong evidence in favor of the view that *Caeoma interstitiale* Schlecht. and *Puccinia Peckiana* are connected. Fischer (5) explains the seeming contradiction between his results and those of the writer by assuming that we have been working with two different fungi. According to this view there would be two orange rusts on the blackberries of America: one the aecidial stage of *Gymnoconia interstitialis*, the other a short-cycled rust closely related to the genus *Endophyllum*. So far as known the short-cycled rust, which we may refer to under the name *Caeoma nitens* Burrill, does not occur in Europe. The fact that there, both are limited to the same low-growing wild species of *Rubus* is evidence in favor of such an assumption. *Puccinia Peckiana*, however, is not uncommon in several different parts of America, and we must expect to find its aecidial stage in these localities.

If there are, then, two orange rusts on the blackberries of the United States it would seem highly interesting and important to study them side by side in order to determine whether in addition to the difference in the way their aecidiospores germinate there are to be found morphological differences between the two Caeomas. The object of this paper is to bring the evidence which shows that we have two orange rusts on the American blackberries and to give a brief comparison of the two forms which have previously been confused and supposed to be one and the same rust.

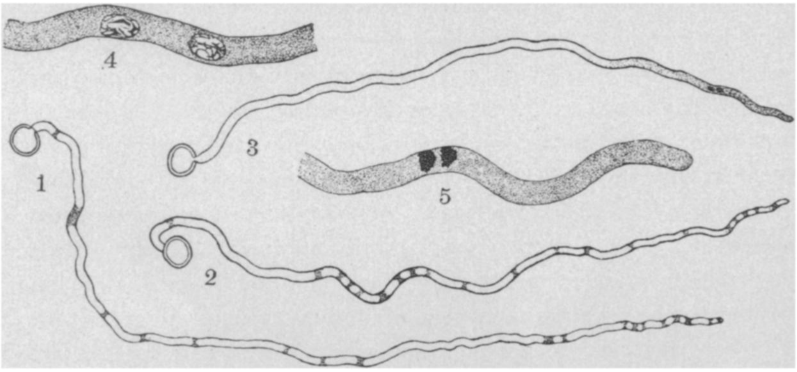
OBSERVATIONS

It was in the hope of obtaining material for testing Fischer's assumption that the writer, at the suggestion of and in company with Professor R. A. Harper, made a trip to the White Mountains of New Hampshire. Here in the vicinity of the village of Glen the writer had on two previous occasions marked spots where the wild blackberry plants were infected with *Puccinia Peckiana*. On visiting these spots June 28, 1916, we found the plants well infected with a *Caeoma*. So far as we were able to determine macroscopically this *Caeoma* had all the characteristics of *Caeoma nitens*. The young infected shoots were chlorotic and somewhat taller than the normal ones. Many of the infected leaves were more or less deformed just as may be observed in the case of plants diseased with *Caeoma nitens*. Spermogonia were present in great abundance. Several infected plants and a considerable number of well-infected leaves were taken to New York City. The plants were put into flower pots and placed in a greenhouse, the purpose being to find out whether they would produce teleutospores later in the summer.

In order to test the germination of the aecidiospores they were dusted over the surface of tap water in Petri dishes. Twenty-one cultures were thus made and incubated at room temperature (about 25° C.). In twenty-four hours most of the spores had germinated. They produced long germ tubes having all the characteristics of aecidiospore germ tubes. No cross walls were to be found and no branches that might be taken for elongated sterigmata. The twenty-one cultures of germinating aecidiospores were carefully observed under the microscope and in only one case must an exception be noted. One spore was found which had put forth a long germ tube that branched into two parts. On one of these branches two quite normal sporidia were borne on typically formed sterigmata. It is difficult to explain this case. Either the spore which gave the promycelium was a contamination or the aecidiospores of *Gymnoconia interstitialis* are in rare instances capable of functioning as teleutospores. The writer is inclined to the latter view.

In order to further test the germination of these aecidiospores a second sowing was made. This time the spores were dusted over the surface of three plates of tap water and three plates of Beyerinck agar. At the same time material of *Caeoma nitens* on *Rubus frondosus* Bigel. was brought into the laboratory from Van Cortlandt Park. These spores were also dusted over the surface of three plates containing tap water and three plates of Beyerinck agar. All of the cultures were made at the same time, on the same media and all were incubated at room temperature. A large percentage of the spores germinated in each of the cultures. The aecidiospores brought from New Hampshire produced long non-septate germ tubes that resemble in every way the germ tubes of other rust aecidiospores. Somewhat better germination was obtained on the agar than on the tap water, but the manner of germination was the same on the two media. The spores brought from Van Cortlandt Park gave practically one hundred per cent. germination and they produced in all cases promycelia.

Having used up all of the aecidiospores brought from New Hampshire in germination and inoculation experiments a second trip was made to Glen on July 7. This time the *Caeoma* was collected from three different localities and on two species of *Rubus*, namely, *Rubus canadensis* L. and *Rubus nigrobaccus* Bailey. Many cultures were made from the aecidiospores obtained from the three different localities. In each case a high per cent. of the spores germinated and they all produced long non-septate germ tubes like those shown in FIGS. 1 and 2. In order to study the nuclear behavior in the germ tubes a considerable quantity of germinating spores was fixed and stained according to a method outlined in an earlier paper (7). A study of the stained material shows that the long tubes typically contain two nuclei. These nuclei lie close together near the end of the tube as is shown in FIG. 3. Sometimes they are separated by a distance of two or three hundred microns but they are never very far apart. The close proximity of the nuclei suggests that these germ tubes would give rise to sporophytic mycelium. The bases of the tubes appear quite empty while the protoplasm shows more and more density as we pass toward their apices. This is well shown in FIG. 3. The nuclei are strikingly large. They often show almost as great a diameter as the tubes that contain them. In some cases they have the appearance of ordinary resting nuclei with a distinct nuclear membrane and blue staining chromatin strands. Such nuclei are illustrated in FIG. 4. In other cases, however, it is difficult to make out a nuclear membrane; the chromatin strands are quite dense and stain so deeply that the whole nucleus appears a dark blue color. Such nuclei are illustrated in FIG. 5. In no case have nucleoli been observed and nuclear division figures seem to be absent from the preparations. One tube was found that had three nuclei, but this is a very rare case. The length of the germ tubes, the presence of only two nuclei, the large size of the nuclei, the absence of division figures and the lack of septa are all char-



GYMNOCONIA INTERSTITIALIS (Schlect.) Lagerh.

FIGS. 1 and 2 show the long unbranched aecidiospore germ tubes as they appear in the living condition, × 175. FIG. 3 shows a germ tube stained; the two nuclei lie near the end of the tube where the protoplasm is dense, × 175. FIG. 4 shows the nuclei in the resting condition; nuclear membranes and chromatin strands are clearly seen, × 590. FIG. 5 shows the deep-staining nuclei; nuclear membranes are not to be observed and chromatin strands are indistinct, × 590.

acteristics which show that these spores in their germination function as aecidiospores. The appearance and behavior of the nuclei in the tubes is in striking contrast to what was observed in the study of the germination of the spores of *Caeoma nitens* (6, 7).

The germination tests show that the aecidiospores brought from New Hampshire function in an entirely different way from those collected in the vicinity of New York City. An experiment was next performed for the purpose of determining whether they would infect wild blackberry plants growing in this region and whether or not they would give rise to the teleuto-stage of *Gymnoconia interstitialis*. A number of plants of *Rubus villosus* Ait. and *Rubus argutus* Link found growing wild in the Bronx, New York City, were transplanted to flower pots and placed in a greenhouse. After they had recovered somewhat from wilting due to the cutting of the larger roots, nine plants of *Rubus villosus* Ait. and three plants of *Rubus argutus* Link, were placed in a moist chamber after being dusted with aecidiospores brought from New Hampshire. Unfortunately most of the spores had been used in the germination tests and only a limited quantity of the material was left for the infection work. An equal number of plants of each of the species used in this experiment were left uninoculated and served as checks. The plants were inoculated on the afternoon of July 1 and were left in a damp chamber for twenty-four hours. They were then placed in the open greenhouse beside the uninoculated plants. On August 15, all of the plants were carefully observed. One plant of *Rubus argutus* Link, was found to bear sori of *Puccinia Peckiana*. Only four leaves were infected but each of these showed numerous sori. All of the other plants appeared quite healthy and showed no signs of infection. It is difficult to understand why more of the plants inoculated did not become infected, but Liro (9) and Fischer (5) both report similar experiences with *Gymnoconia*. The check plants were all quite free of rust. Since *Puccinia Peckiana* has never been found on the blackberry plants in the vicinity of New York City we must assume that the plants brought into the greenhouse from the Bronx were free from this rust and that the infection obtained was the result of sowing the aecidiospores of the New Hampshire *Caeoma*. This experiment confirms the results of Tranzschel (13), Clinton

(3), Liro (9), and Fischer (5). Without a doubt, *Puccinia Peckiana* is the teleuto-stage of *Gymnoconia interstitialis*. The plants of *Rubus canadensis* L. that were brought here from New Hampshire bearing the *Caeoma* and planted out in flower pots were on August 15 found to be well infected with teleutospores of *Gymnoconia*. These results, together with the germination tests, seem to show conclusively that the orange rust common on wild blackberries in the vicinity of Glen, New Hampshire, is *Gymnoconia interstitialis*.

It seems proper to report at this point an infection experiment with *Caeoma nitens*. This experiment was performed in 1913 and 1914, but has not previously been reported. Sixteen plants of *Rubus villosus* Ait. found growing wild in Van Cortlandt Park were transplanted to flower pots and placed in a greenhouse. The plants were all quite free from rust infection and no infected plants were observed near where they were found growing. They were brought into the greenhouse the latter part of June. Ten of the plants were well dusted with the spores of *Caeoma nitens* and placed under bell jars for about one week. They were then placed in the open greenhouse. The other six plants were left uninoculated and were used as checks. No infection was observed on any of the plants during the summer and fall of 1913. In the spring of 1914, however, the young shoots of three of the plants that had been inoculated the preceding summer bore leaves well infected with *Caeoma nitens*. None of the check plants gave any infected shoots. The experiment shows that the spores of *Caeoma nitens* are capable of infecting new plants. It further shows that the *Caeoma* can reproduce itself without an intermediate stage. A similar experiment was performed in which the teleutospores of *Gymnoconia interstitialis* were used instead of the functional teleutospores (aecidiospores) of the short-cycled form. Ten plants of *Rubus procumbens* were inoculated by scraping teleutospores from mature sori with a wet knife blade and then smearing them over the surface of the leaves and young shoots. The plants thus inoculated were kept under bell jars for one week and then placed in the open greenhouse. They have been under observation for more than two years but the plants have not become infected. The viability of the spores was shown by germination tests and the writer is unable to explain why infection did not result. The experiment should be repeated.

After being fully convinced that the orange rust, so common around New York City, is functionally different from the one in New Hampshire a special effort was made to discover possible morphological differences between the two forms. Infected plants from the two sources were placed side by side and carefully compared. Special notice was taken of the color of the spores in mass, the size and distribution of the Caeomas, the effect on the host, etc. Material of both forms was fixed in Flemming's weaker solution, embedded in paraffin in the usual way, sectioned with a microtome and studied under the microscope. Spermogonia are abundant in both cases. Their form, size and distribution was noted as well as the size and shape of the spermatia. In both forms the aecidiospores are born in chains with intercalary cells. The spores from the two sources were compared as to size, shape, content, thickness of spore wall and spore wall markings. Fifty ripe aecidiospores from the New Hampshire material were chosen at random and measured along their greatest diameters. The average diameter for the fifty spores was found to be 25.25 μ. Fifty aecidiospores of *Caeoma nitens* were likewise chosen and measured in the same way. Here the average diameter was found to be 25.29 μ. The difference obtained is not great and may well be attributed to errors in making the measurements.

This comparative study has failed to disclose either macroscopic or microscopic morphological differences between the two rusts. So far as the writer has been able to observe both are exactly alike morphologically. Only after having germinated the spores is it possible to distinguish between the two forms.

DISCUSSION

The close morphological and pathological similarity between two apparently different rusts at once raises the question as to whether or not they are genetically related. Do we have here a case of parallelism or has one of the Caeomas been derived from the other? It is possible to conceive that two rusts living on the same hosts may after a time show similar morphological characteristics, but it is hard to think they would become so much alike as to be morphologically indistinguishable. If we consider only the life cycles of the two forms we find that they belong in groups that are rather widely separated in our classifications of the rusts. The short-cycled *Caeoma nitens* we would place near the genus *Endophyllum; Gymnoconia interstitialis* belongs near *Phragmidium.* Arthur (1) puts *Gymnoconia* in the Aecidiaceae while *Endophyllum* he places in the Uredinaceae. When we consider the two rusts from a morphological standpoint we find that in their *Caeoma* stage they are alike and we are inclined to consider them related forms. Werth (14) believes the aecidiospores of *Endophyllum Sempervivi* are capable of functioning either as aecidiospores or as teleutospores, according to the conditions under which they germinate. Maire (10) reports a variety of *E. Sempervivi* that regularly produces ordinary aecidiospore germ tubes. These suggestions are interesting in this connection and they deserve consideration in our studies of the two orange rusts. The finding of a basidium in cultures of the aecidiospores of *Gymnoconia interstitialis* offers a further suggestion and leads the writer to believe that the two rusts may be related. If a strain of the orange rust could be found in which some of the aecidiospores germinate by ordinary germ tubes while others produce promycelia the question as to the relationship of the two forms would be much clearer. An effort should be made to find such an intermediate strain.

The two Caeomas have undoubtedly been confused in this country. There is no way of knowing which rust Burrill (2) described as *Caeoma nitens* since it seems that both occur in the vicinity of Urbana, Illinois. Both are reported from Missouri and it is impossible to determine which form Newcombe and Galloway (11) used in their work. From their drawings of the germinating spores, however, one would guess that they had the short-cycled form. It is also probable that the material used by Olive (12) in his study of sexual cell fusions in the rusts was *Caeoma nitens*, but of this we can not be sure.

As one looks over the group of host species as given by Arthur (1) the question presents itself as to which ones are really host species for *Gymnoconia* and which ones are the host species of *Caeoma nitens.* This list undoubtedly includes the hosts of both rusts and it is not possible in any given case to determine with certainty which rust was collected. Since *Gymnoconia* occurs on *Rubus saxatilis* and *R. arcticus* in Europe it seems natural to assume that the *Caeoma* on related species in this country belongs to *Gymnoconia*. It is probable, therefore, that the orange rust on the low-growing *R. arcticus* L. of Yukon, *R. stellatus* Smith of Alaska, and *R. triflorus* Richardson or *R. americanus* Britton of New Hampshire and Wisconsin will prove to be *Gymnoconia*. The writer has collected *Gymnoconia* on *R. frondosus* Bigel., *R. canadensis* L. and *R. nigrobaccus* Bailey. These are all upright-growing species and it may be that the orange rust on many of the other upright species is *Gymnoconia*. The writer feels inclined to think, however, that *Caeoma nitens* is the more common of the two rusts and that it will prove to have a wider range of host species than *Gymnoconia*. According to Clinton (3) the *Caeoma* has been reported from Carolina, Connecticut, Georgia, Illinois, Iowa, Kansas, Maryland, Massachusetts, Minnesota, Mississippi, Missouri, Nebraska, New Hampshire, New Jersey, New York, Ohio, Pennsylvania, Texas, West Virginia and Wisconsin while the teleuto-stage is reported from only four states: Illinois, Massachusetts, Missouri and New York. The orange rust in most of those states where the teleuto-stage has not been found is probably *Caeoma nitens*. New Hampshire, however, must be mentioned as an exception, since the rust common in that state has proven to be *Gymnoconia*. The fact that the orange rust is much more conspicuous than the teleuto-stage may to some extent account for its being more often reported. Only a careful study of the distribution and host limitations of the two forms in the several states can furnish grounds for definite conclusions. Nevertheless we may predict that the orange rust reported on *R. cuneifolius* Pursh, *R. occidentalis* L., *R. Randii* (Bailey) Rydb., *R. strigosus* Michx., *R. trivialis* Michx., *R. villosus* Ait., *R. vermontanus* Blanch. and *R. vitifolius* Cham. & Schlecht. is *Caeoma nitens*.

So far as is at present known the short-cycled orange rust does not occur in Europe. Before accepting this conclusion, however, a careful study of the manner of germination of the aecidiospores from various localities should be made. Special attention should be given to the *Caeoma* in those sections where the teleuto-stage of *Gymnoconia* has not yet been found. Lageheim's (8) suggestion, "dass das *Caeoma* sich reproduciren kann," is interesting in this connection. He writes: "Aus mehreren Gründen scheint es mir nun nicht unmöglich, dass die Aecidien unserer Gymnoconia sich zu reproduciren vermögen. Während dieselben nämlich an vielen Orten des europäischen und asiatischen Russlands, im nördlichen, mittleren und südlichen Schweden und bei München gefunden worden sind, so sind die dazu gehörenden Teleutosporen (in Europa) nur bei Kuikkjokk im Schwedisch-Lappland, bei St. Petersburg und Moskau beobachtet worden." The orange rust of Europe seems to be of no economic importance and so far as the writer knows has not been found on cultivated blackberries or raspberries. This suggests that the rust so often reported as doing great damage to cultivated blackberries and raspberries in the United States is the short-cycled form. The writer has twice collected the orange rust on cultivated blackberries and in both cases it proved to be *Caeoma nitens*. It would be an interesting experiment to determine whether *Gymnoconia* is capable of infecting our cultivated blackberries and raspberries. This and many other experiments that suggest themselves must be left for future studies. Questions as to which of the two forms is the more primitive and as to what environmental conditions may have led to the development of two rusts with such different life histories and yet so much alike morphologically must at present be left unanswered. Both forms deserve further study.

SUMMARY

1. There are two forms of the orange rust on the blackberries of the United States. One is the *Caeoma*-stage of *Gymnoconia interstitialis* (Schlecht.) Lagerh.; the other is a short-cycled rust with a life history like the Endophyllums as described by Arthur (1).

2. The two rusts are morphologically alike in their *Caeoma*-stage though so different in their life histories.

3. The germination of the *Caeoma* spores is in the one case (*Caeoma nitens*) teleutoid, in the other (*Gymnoconia interstitialis*) it is just as typically aecidioid.

4. It is impossible at present to determine in the numerous references to orange rust of blackberries which form was under

observation except in a few cases where germination tests or infection experiments were made.

5. The short-cycled *Caeoma nitens* seems more widespread in the United States than *Gymnoconia interstitialis*.

6. It seems to be the short-cycled form of the orange rust that is so destructive to our cultivated blackberries and raspberries in this country.

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